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CHROMOSOME NUMBERS IN THE COMPOSITAE. IX AFRICAN SPECIES

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ABSTRACT

Eighty species of African Compositae are examined and their chromosome counts tabulated.

INTRODUCTION

Previous contributions to this series have dealt with species from North America. Bud material and voucher specimens on which the present paper is based were collected by the junior author in 1962–63 while engaged in field work in Africa.

Chromosome counts were made from pollen mother cell squashes. Buds were collected from plants growing in the field and placed in a freshly mixed solution of 4 parts chloroform: 3 parts absolute alcohol: 1 part glacial acetic acid, and allowed to remain for a period varying from one to several weeks. Young anthers were subsequently removed and squashed in acetocarmine. Camera lucida drawings were made at an initial magnification of *ca.* 2000 diameters.

Vernonieae

Vernonia ($x = 9, 10, 16, 17$). This predominantly pantropical genus is reportedly composed of over 500 species (Gleason, 1923). Including the present counts, approximately 16 species are known chromosomally (Cave, 1956–61). In spite of this limited sampling, several basic chromosome numbers have emerged. African species of the Sections *Strobocalyx* and *Decaneurum* are known with $n = 9$ and $n = 10$, respectively. The American Section *Lepidaploa* has at least one species with $n = 17$ (Turner, unpublished); the South American species, *V. nudiflora* Less., of this same Section, is reported with $n = 16$ (Cave, 1959) while *V. platensis* Less. is reported with $n = 20$ (Cabrera, 1944). Chromosome counts for the widespread pantropical taxon, *Vernonia cinerea*, which is the sole species of the Section *Tephrodes*, have been reported from 3 different continents as diploid with $n = 9$ (Africa: Miege, 1960, and present paper; Asia: Chuang *et al.*, 1962; Grant, 1953; and North America: Turner & King, 1964). Our counts for *Vernonia glabra* ($n = 10$) agree with that reported by Riley and Hoff (1961). In view of the limited number of counts available, it would be premature to assess the value of chromosome numbers as systematic guides within *Vernonia*, but it is obvious that the variation already described is sufficiently interesting to warrant a more intensive cytological investigation of the genus.

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Chromosome counts for *Erlangia* ($n = 10$) and *Ethulia* ($n = 10, 20$) are first reports for these genera.

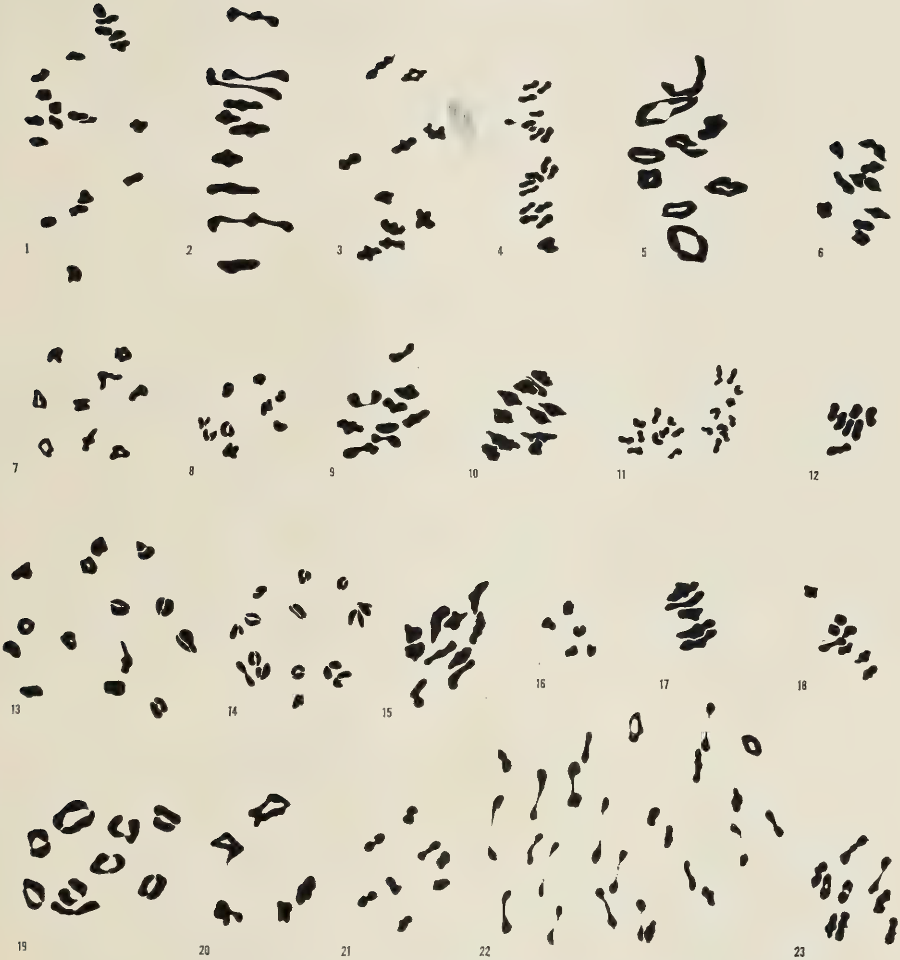
Eupatorieae

Ageratum conyzoides ($n = 20$). Collections of this widespread, weedy, species have been reported as tetraploid from India (Mitra, 1947), Central America (Turner, unpublished) and Africa (present paper). Darlington and Wylie (1956) list only a single diploid count ($n = 10$) for the taxon, reported by a Japanese worker in 1916.

Mikania cordata ($n = 18$). Mangenot and Mangenot (1957) have reported two other African collections of this species to be diploid with $n = 18$ (reported as *M. scandens*). Mitra (1947) reported the chromosome number of *M. cordata* to be $2n = 38$; however, the drawing documenting his count is not convincing since it appears to show $2n = 36$. Our meiotic figure (Table 1) shows 18 bivalents. One of the bivalents is quite large and might be interpreted as two overlapping chromosome pairs; however, since a number of metaphase meiotic cells from the same bud showed essentially the same chromosomal configuration, we feel the number $n = 18$ to be the correct interpretation. Turner *et al.* (1962) have reported a chromosome number of $n = 17$ for *Mikania gonzalezii*, the only other species of the genus for which counts are available.

Astereae

Aster subulatus ($n = 10$). This now widespread, weedy species is native to North and South America. The senior author has counted at least 10 collections from 5 Mexican states and Guatemala; all were diploid with $n = 5$. A closely related taxon, *A. squamatus* (Spreng.) Hieron., from Argentina is reportedly tetraploid with $n = 10$ (Darlington and Wylie, 1956). Shinners (1953) treated this latter species as synonymous with *A. subulatus* var. *australis* (Gray) Shinners, the more common populational form of *A. subulatus* in South America. It would appear that the present material (Table 1) if introduced into Swaziland, was from that region. Huziwara (1958) has reported *A. subulatus* to be diploid with $2n = 18$ (or $n = 9$); his material was reportedly collected at Kobe, Japan. Huziwara's counts should be held suspect until his voucher material, if available, can be examined; in any case, his figures showing the karyotypes of *A. subulatus* and the very closely related, if not conspecific, *A. exilis*, are very different and if his material is correctly determined, some interpretation would be in order.



FIGS. 1-23

Meiotic chromosomes of species of Compositae, Xca. 2000:
1. *Ethulia conyzoides* ($n = 20$)—2. *Vernonia aemulans* ($n = 10$)—3. *Vernonia glabra* ($n = 10$)—4. *Mikania cordata* ($n = 18$)—5. *Aster bakeranus* ($n = 9$)—6. *Aster subulatus* ($n = 10$)—7. *Nidorella hottentotica* ($n = 9$)—8. *Nidorella resedifolia* ($n = 9$)—9. *Nidorella welwitschii* ($n = 9$)—10. *Blumea mollis* ($n = 11$)—11. *Geigeria burkei* ($n = 10$; metaphase, division II)—12. *Helichrysum decorum* ($n = 7$)—13. *Coreopsis grandiflora* ($n = 14$)—14. *Melanthera scandens* ($n = 15$)—15. *Inezia integrifolia* ($n = 10$)—16. *Senecio discifolius* ($n = 5$)—17. *Senecio hockii* ($n = 5$)—18. *Berkheya setifera* ($n = 8$)—19. *Haplocarpha scaposa* ($n = 9$)—20. *Hirpicium diffusum* ($n =$ ca. 5)—21. *Ursinia nana* ($n = 8$)—22. *Gerbera discolor* ($n = 25$)—23. *Heterachaena massavensis* ($n = 9$).

Microglossa angolensis (n = ca. 18). The taxon apparently possesses both diploid and tetraploid population and/or individuals since Mangenot and Mangenot (1962) reported a diploid collection from Africa with $n = 9$. Chuang *et al.* (1962) have also reported an asiatic species of *Microglossa* with $n = 9$.

Chromosome counts for the genera *Dichrocephala* ($n = 9$), *Nidorella* ($n = 9$), and *Psiadia* ($n = 9$) are first reports.

Inuleae

Blumea mollis ($n = 11$). Only 3 counts are available for the genus. Shetty (1961) has reported an Indian species to be diploid with $n = 10$ and Chuang *et al.* (1962) have reported a Taiwanian species with $n = 10$. Chromosome counts for *Geigeria* ($n = 10$) have not been reported previously.

Heliantheae

Chromosome counts (Table 1) for species of *Coreopsis* ($n = 14$), *Melanthera* ($n = 15$), *Spilanthes* ($n = 13, 26$) and *Tridax* ($n = 18$) agree with previously reported counts for these genera (Darlington and Wylie, 1956; Turner *et al.*, 1961).

Anthemideae

Chromosome counts for 20 of the approximately 55 genera of this tribe have been reported. Basic numbers of $x = 8, 9, 17$ or combinations of these have been found for all of the taxa except *Cotula* with $x = 10$ and 13 (Hair, 1962; a base number of $x = 5$ was hypothesized but species at the $n = 5$ level have not been reported), *Centipeda* (Hair, 1963), and *Inezia* (Table 1). The latter 2 genera have basic numbers of $x = 10$.

Senecioneae

The chromosome counts for *Senecio abyssinicus*, *S. discifolius*, and *S. hockii* are noteworthy in that they are diploid with $n = 5$. All other species of *Senecio* examined to date have had chromosome numbers on a base of $x = 10$[3], 22, 23 or 24. Most workers, including Arano (1962), have postulated an ancestral basic number of $x = 5$ for the genus (and tribe); Ornduff *et al.* (1963), however, have proposed an ancestral basic number of $x = 10$ for these taxa, the number $x = 5$ having been derived through aneuploid loss. Their argument stems primarily from the observation that taxa with $x = 5$ are rare (found in only 5 or 6 annual species of the closely related genera *Senecio* and *Emilia*). They further argue that polyploid taxa with odd numbers of $n = 15, 25$, etc. are not common in the genus, and these should be relatively common if the basic number were $x = 5$.

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[3] A single species, *S. arenarius*, is known to possess $n = 9$. According to Afzelius (1949) this species "belongs to the flora of the Cape Province and is often cultivated in gardens . . . It resembles *S. elegans* L. which has $n = 10$ and also originates from the Cape Province."

Senecio, with over 2,000 species, is probably the largest and most widely distributed genus of vascular plants. Hoffmann (1894) treated the taxon as consisting of 2 subgenera, *Emilia* and *Senecio*. Chromosome numbers of $n = 5$ and $n = 10$ have been found in both of these subgenera. Species with chromosome numbers of $n = 9$[3], 8, 7 or 6 have not been reported, in spite of the fact that diploid taxa with $n = 10$, at least in Africa, are relatively common. In such a large successful genus, one would expect at least some species with chromosome numbers of 6 through 8 to have persisted, especially if the taxa with $n = 5$ are of relatively recent origin. Actually, Ornduff *et al.* admit to the tetraploid nature of $n = 10$ in *Emilia*; presumably the basic number for this genus is $x = 5$. But since *Emilia* may be treated on morphological grounds as a subgenus of *Senecio* and since the subgenus, *Senecio*, also has species with $n = 5$ and 10, it would appear more consistent with reason to accept a base of $x = 5$ for *Senecio* also. Obviously if future workers find species of *Senecio*, which are closely related to the $n = 5$ species, with n numbers of 9, 8, 7 or 6, arguments for a basic number of $x = 5$ would be weakened. Commonness of a character is not in itself an indication of primitiveness. Indeed if a primitive character, in this case an ancestral chromosome set, is to be preserved within a rapidly evolving, successful phylad, the character concerned ought to be rare[4]. As concerns the preservation of an ancestral diploid genome in a group like *Senecio*, one would expect such a set to be retained in those taxa which are morphologically "advanced", for the ancestral morphological forms ought to be retained best in those taxa which are at the polyploid level where multiple genes might form effective "buffers" (Stebbins, 1950) against additional morphological changes due to mutational forces.

It is not difficult to account for the absence of taxa with numbers of $n =$ 15, 25, etc., if one can accept the tetraploid nature of species with $n = 10$. To obtain taxa with $n = 15$ would require the gametic combinations of $n =$ 10 and $n = 5$: a sporophytic triploid condition such that 5 univalents would be expected at meiosis and even if complete autosyndesis somehow occurred there would still be an odd univalent which might cause effective selection against the establishment of triploid individuals (Darlington, 1956). This same reasoning can be used to account for the general absence of taxa with n numbers of 25, 35, etc. Triploids and/or pentaploids on a base of $x = 5$ might be expected in the genus *if* apomixis were a factor in the speciation process; (cf. *Erigeron* with $n = 9, 18, 27$, etc.) but so far as we are aware apomixis has not been reported in the genus.

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[3] For example, well defined phyllaries (or chaff) on the receptacle is looked upon as a primitive character. In the very natural genus *Hymenoppappus* ($x = 17$) with 25 taxa, only a single species possesses chaff (Turner, 1956). In the Compositae generally, chaff is the exception rather than the rule (even the more woody species lack chaff, e.g., *Baccharis*); yet hardly any current worker questions the assumption that naked receptacles are the more advanced.

Arctotideae

Berkheya ($n = 8$). Two other species are reported to have chromosome numbers of $n = 7$ (Darlington and Wylie, 1956). The chromosome counts for species of *Haplocarpha* ($n = 9$), *Hirpicium* ($n =$ ca. 5) and *Ursinia* ($n = 8$) are new generic reports.

Mutisieae

Gerbera discolor ($n = 25$). Including the present, only four species of this genus have been counted (Darlington and Wylie, 1956): two Asiatic species, belonging to the Section *Gerbera*, are diploid with $n = 23$; while two African species, belonging to the Section *Lasiopus*, are diploid with $n = 25$.

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TABLE 1

Species of Compositae examined for Chromosome Number

Tribe Vernonieae

Species	Location and Voucher	n Number
Erlangea cordifolia (Benth. ex Oliv.) S. Moore	KENYA: Central Prov., Royal Nairobi National Park, *Lewis* 5945.	*ca.* 10 *ca.* 10
Erlangea tomentosa S. Moore	KENYA: Coast Prov., Taita Dist., S.E. Slope of Mt. Vuria, *Lewis* 5936.	10
Erlangea tomentosa S. Moore	TANGANYIKA: Tanga Region, Lushoto Area, Herkulu Tea Estate. *Lewis* 6045.	*ca.* 10*
Ethulia conyzoides L.	UGANDA: Buganda Prov., Mengo Dist., 3.5 miles N.E. of Kampala, *Lewis* 6025.	*ca.* 10*
Ethulia conyzoides L.	S. AFRICA: Natal Prov., Hlabisa Dist., Charters Creek, *Lewis* 6302.	20 (Fig. 1)
Vernonia brachycalyx O. Hoffm.	UGANDA: Northern Prov., Karamoja Dist., base of Mt. Moroto, *Lewis* 5992.	10
Vernonia cinerea (L.) Less.	TANGANYIKA: Tanga Region, Tanga Area, 4 miles N. of Tanga, *Lewis* 6061.	9
Vernonia aemulans Vatke	N. RHODESIA: Northern Prov., Abercorn Dist., 5.5 miles S.W. of Abercorn, *Lewis* 6121.	10 (Fig. 2)
Vernonia glabra (Steetz) Vatke	S. RHODESIA: Salisbury Dist., Salisbury Cranborne, *Lewis* 6256.	10 (Fig. 3)

* Indicates the occurrence of one to several fragments.

Vernonia oligocephala (DC.) Sch. Bip ex Walp.	S. AFRICA: Transvaal Prov., Potgietersrust Dist., 2 miles S.W. of Potgietersrust. *Lewis* 6262.	*ca.* 9	
Vernonia oligocephala (DC.) Sch. Bip. ex Walp.	TANGANYIKA: Southern Highlands Region, Mbeya Area, Mbeya Range, *Lewis* 6073.	*ca.* 20	
Vernonia viatorum S. Moore	N. RHODESIA: Northern Prov. ,Abercorn Dist., Sunzu Gorge, *Lewis* 6095.	10	

Tribe Eupatorieae

Ageratum conyzoides L.	UGANDA: Eastern Prov., Buso Dist., 3 miles W. of Busesa, *Lewis* 6028.	20	
Ageratum conyzoides L.	KENYA: Central Prov., Meru Dist., 8 miles N.E. of Runyenje's, *Lewis* 5912.	20	
Ageratum conyzoides L.	TANGANYIKA: Tanga Region, Tanga Area, 4 miles N. of Tanga, *Lewis* 6060.	20	
Eupatorium africanum Oliv. ex Hiern.	TANGANYIKA: Southern Highlands Region, Iringa Area, 4.5 miles N.E. of John's Corner, *Lewis* 6068.	10	
Mikania cordata (Burm. f.) B. L. Robins.	KENYA: Coast Prov., Taita Dist., Ollaiani River, *Lewis* 6034.	18	(Fig. 4)

Tribe Astereae

Aster bakerianus Burt Davy ex C. A. Smith	S. AFRICA: Natal Prov., Estcourt Dist., 3.2 miles W.N.W. of Estcourt, *Lewis* 6272.	9	
Aster bakerianus Burt Davy ex C. A. Smith	TANGANYIKA: Southern Highlands Region, 7.1 miles E. of Mbeya, *Lewis* 6084.	9	(Fig. 5)
Aster hyssopifolius Berg.	TANGANYIKA: Southern Highlands Region 7.1 miles E. of Mbeya, *Lewis* 6081.	18	
Aster subulatus Michx.	SWAZILAND: Komati River, by Forbes Reef-Piggs Peak Rd., *Lewis* 6327.	10	(Fig. 6)
Conyza aegyptiaca (L.) Ait.	N. RHODESIA: Northern Prov., Abercorn Dist., Abercorn, *Lewis* 6107.	9	
Conyza newii Oliv. & Hiern.	TANGANYIKA: Tanga Region, Lushoto Area, Herkulu Tea Estate, *Lewis* 6050.	9	
Conyza newii Oliv. & Hiern.	KENYA: Coast Prov., Taita Dist., S.E. slope of Mt. Vuria, *Lewis* 5935.	9	
Conyza pinnata (L. f.) O. Ktze.	S. AFRICA: Natal Prov., Lions River Dist., 1 miles S. of Rosetta, *Lewis* 6276.	9	
Conyza podocephala D.C.	S. AFRICA: Transvaal Prov., Pretoria Dist., Pretoria, Wonderboom, *Lewis* 6343.	9	
Conyza steudelii Sch. Bip.	TANGANYIKA: Tanga Region, Lushoto Area, Herkulu Tea Estate, *Lewis* 6038.	9*	
Dichrocephala intergrifolia (L. f.) O. Ktze.	TANGANYIKA: Tanga Region, Lushoto Area, Herkulu Tea Estate, *Lewis* 6041.	9	
Microglossa angolensis Oliv. & Hiern.	TANGANYIKA: Southern Highlands Region, 17 miles N.N.W. of Tukuyu, *Lewis* 6090.	*ca.* 18	
Nidorella auriculata DC.	N. RHODESIA: Northwestern Prov., Mwinilanga Dist., 2 miles W. of Ikelengi, *Lewis* 6191.	9	
Nidorella hottentotica DC.	S. AFRICA: Transvaal Prov., Pretoria Dist., Pretoria, Wonderboom, *Lewis* 6350.	9	(Fig. 7)

Nidorella resedifolia DC.	N. RHODESIA: Northern Prov., Abercorn Dist., Sunzu Gorge, *Lewis* 6096.	9 (Fig. 8)
Nidorella welwitschii S. Moore	ANGOLA: Mexico Dist., 2 miles W. of Jimbe River by Caianda-Mwinilunga Rd., *Lewis* 6217.	9 (Fig. 9)
Psiadia arabica Jaub. & Spach	KENYA: Central Prov., Royal Nairobi National Park, *Lewis* 5940.	9

Tribe Inuleae

Blumea mollis (*D. Don*) Merr.	CONGO: Katanga Prov., Haut-Katanga Dist., 6 miles N.E. of Mokambo, *Lewis* 6127.	11 (Fig. 10)
Blumea mollis (D. Don) Merr.	N. RHODESIA: Southern Prov., Livingstone Dist., Victoria Falls, *Lewis* 6243.	ca. 11
Geigeria burkei Harv.	S. AFRICA: Transvaal Prov., Pretoria Dist., Pretoria, Wonderboom, *Lewis* 6349.	10 (Fig. 11)
Gnaphalium luteo-alba L.	N. RHODESIA: Northern Prov., Abercorn Dist., Chilunoma River, nr. Abercorn. *Lewis* 6111.	7
Helichrysum decorum DC.	S. AFRICA: Natal Prov., Durban Dist., Isipingo Beach, *Lewis* 6289.	7 (Fig. 12)
Helichrysum foetidum (L.) Cass.	TANGANYIKA: Tanga Region, Lushoto Area, Herkulu Tea Estate, *Lewis* 6044.	7
Helichrysum mixtum O. Hoffm.	S. AFRICA: Natal Prov., Hlabisa Dist., 3.7 miles W. of Charters Creek, *Lewis* 6307.	7
Helichrysum panduratum O. Hoffm.	S. AFRICA: Natal Prov., Durban Dist., Isipingo Beach, *Lewis* 6287.	7

Tribe Anthemideae

Anthemis tigreensis J. Gay ex A. Rich.	KENYA: Central Prov., Nanyuki Dist., N.W. slope of Mt. Kenya, *Lewis* 5919.	9
Inezia integrifolia (Klatt) Phillips	S. AFRICA: Transvaal Prov., Barberton Dist., 21 miles S.E. of Barberton, *Lewis* 6336.	10 (Fig. 15)

Tribe Heliantheae

Aspilia africana (Pers.) Adams	KENYA: Coast Prov., Taita Dist., Ollaiani River, *Lewis* 6035.	34 ± 2
Bidens pilosa L. var. *minor* Sheriff	TANGANYIKA: Tanga Region, Lushoto Area, Herkulu Tea Estate, *Lewis* 6043.	38 ± 2
Bidens taitensis Sheriff	KENYA: Coast Prov., Taita Dist., S.E. slope of Mt. Vuria, *Lewis* 5934.	23 ± 1
Coreopsis grandiflora Nutt.	SWAZILAND: Mbabane, Mbabane River, *Lewis* 6319.	14 (Fig. 13)
Galinsoga parviflora Cav.	ETHIOPIA: Harar Prov., N.W. edge of Lake Alemaya, *Lewis* 5875.	ca. 8
Melanthera scandens (Schumach. & Thonn.) G. Roberty	KENYA: Coast Prov., Taita Dist., Ollaiani River, *Lewis* 6033.	15 (Fig. 14)
Spilanthes mauritiana (Rich. ex Pers.) DC.	UGANDA: Northern Prov., Karamoja Dist., base of Mt. Moroto, nr. Moroto, *Lewis* 5994.	13
Spilanthes uliginosa Sw.	TANGANYIKA: Tanga Region, Tanga Area, 7 miles N. of Tanga *Lewis* 6054.	ca. 26
Tridax procumbens L.	KENYA: Coast Prov., Taita Dist., Kyanite Mine, *Lewis* 6037.	18